Morphology and Putative Ecology of Eocene Ant Agroecomyrmex duisburgi (Hymenoptera: Formicidae: Agroecomyrmecinae)

Authors: Radchenko, Alexander, and Khomych, Mykola

Source: Annales Zoologici, 72(2) : 261-268

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/00034541ANZ2022.72.2.009

MORPHOLOGY AND PUTATIVE ECOLOGY OF EOCENE ANT *AGROECOMYRMEX DUISBURGI* (HYMENOPTERA: FORMICIDAE: AGROECOMYRMECINAE)

ALEXANDER RADCHENKO[1,*] and MYKOLA KHOMYCH[2]

[1]*Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine*
e-mail: agradchenko@hotmail.com / ORCID.org/0000-0002-8850-0530
[2]*Village Voronky, Volodymerets Distr., Rivne Prov., Ukraine*
**corresponding author*

Citation: Radchenko, A., Khomych, M. 2022. Morphology and putative ecology of Eocene ant *Agroecomyrmex duisburgi* (Hymenoptera: Formicidae: Agroecomyrmecinae). Annales Zoologici, 72: 261–268. doi: 10.3161/00034541ANZ2022.72.2.009

Received: 23 April 2022 **Accepted**: 25 May 2022 **Printed**: 30 June 2022

Abstract.— Agroecomyrmecinae is a poorly-known subfamily of ants that includes just two extant genera and species, *Tatuidris tatusia* Brown et Kempf, 1968, a leaf-litter dweller from the Neotropics, and A*nkylomyrma coronacantha* Bolton, 1973, an arboreal inhabitant from West Africa. Two Agroecomyrmecinae genera have been described from Eocene fossils: *Agroecomyrmex* Wheeler, 1910 found in European amber (Baltic and Bitterfeld), and *Eulithomyrmex* Carpenter, 1935 found in North American shale (Florissant). There are published records of just seven specimens of *Agroecomyrmex duisburgi* (Mayr, 1868), the sole member of its genus. We found four additional *A. duisburgi* specimens, three from Baltic amber and one from Rovno (Ukraine) amber of similar age (Priabonian stage, 37.8–33.9 Ma). This increases number of known ant subfamilies in Rovno amber to 10, and indicates that Agroecomyrmecinae were distributed in the late Eocene on both the northern and southern coasts of the Paratethys Sea. Based on morphological features and the rarity of fossil remains, we suggest that *Agroecomyrmex* and *Eulithomyrmex* were most likely neither litter-dwelling nor arboreal, but were epigean species, living on the soil surface.

Key words.— Ants, *Agroecomyrmex*, *Eulithomyrmex*, *Tatuidris*, *Ankylomyrma*, fossils, late Eocene, Rovno amber, first record, morphology, behavior, evolution

INTRODUCTION

Agroecomyrmecinae is a poorly-known subfamily of ants that includes just two extant genera and species, *Tatuidris tatusia* Brown et Kempf, 1968, a leaf-litter dweller from the Neotropics, and *Ankylomyrma coronacantha* Bolton, 1973, an arboreal inhabitant from West Africa. Two Agroecomyrmecinae genera have been described from late Eocene fossils: *Agroecomyrmex* Wheeler, 1910 found in European amber (Baltic and Bitterfeld), and *Eulithomyrmex* Carpenter, 1935 found in North American shale (Florissant).

PL ISSN 0003-4541 © Museum and Institute of Zoology PAS
doi: 10.3161/00034541ANZ2022.72.2.009

In the course of our ongoing investigations of ants in Rovno amber (Priabonian stage, 37.8–33.9 Ma) from Rivne Oblast (province), Ukraine, we encountered a worker specimen we identified as Agroecomyrmecinae, a subfamily previously unknown from this amber. Rovno amber, named after the city of Rivne (formerly Rovno), is found in the Rivne Oblast and nearby areas of Ukraine and Belarus. To date, 77 ant species from 39 genera and nine subfamiles have been recorded from Rovno amber (Dlussky and Rasnitsyn 2009; Perkovsky 2016; Radchenko and Dlussky 2016, 2018a, 2018b, 2019; Radchenko *et al*. 2018; Radchenko and Perkovsky 2018, 2020; Radchenko and Khomych 2020; Radchenko 2020, 2021; Radchenko *et al*. 2021; Radchenko and Proshchalykin 2021; Radchenko and Khomych, in press).

We identified the specimen as *Agroecomyrmex duisburgi* (Mayr, 1868). This species was described from late Eocene Baltic amber (Priabonian stage). Dlussky and Rasnitsyn (2009) later recorded this species in Bitterfeld amber (Germany, Saxony) of similar age. In the late Eocene, these areas were on the northern coast of the Paratethys Sea, while Rovno amber was on the southern coast.

Material and methods

There are published records of just seven specimens of *Agroecomyrmex duisburgi*, the sole member of its genus (Dlussky and Rasnitsyn 2009). We found one more specimen for the first time in Rovno amber plus three more specimens from Baltic amber in the collection of Jonas Damzen (Lithuania). For the present study, we examined two *A. duisburgi* worker specimens: one in a piece of Rovno amber from the Volodymerets district, Rivne province, Ukraine (collection number F-652), and one in a piece of Baltic amber (collection number JDK 4522). Both specimens are intact and well preserved. The specimen from Rovno amber is deposited in the collection of M. Khomych; the Baltic amber specimen is in the collection of Jonas Damzen.

The photographs were taken with a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with the LAS Core software. Specimens were measured using a Leica MZ6 stereomicroscope with an ocular-micrometer at a maximum magnification x100. Not all features of the examined specimen were properly visible and measurable, so we measured only well visible details (calculated with an accuracy of 0.01 mm). We measured:

HL – maximum length of the head in dorsal view, measured in a straight line from the anteriormost point of clypeus to the mid-point of occipital margin;

SL – maximum length of the scape measured in a straight line from its apex to the articulation with condylar bulb;

OL – maximal diameter of the eye;

ML – diagonal length of the mesosoma seen in profile from the anterior margin of neck shield to the posterior margin of propodeal lobes;

MH – height of the mesosoma, measured from the upper level of promesonotum perpendicularly to the level of lower margin of mesopleuron;

PL – maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;

PH – maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole;

PPL – maximum length of postpetiole from above;

PPH – maximum height of postpetiole (including ventral lobe) in profile;

ESL – maximum length of the propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of the spine;

HTL – maximum length of the metatibia.

Total length is calculated as the sum of HL + ML + PL + length of the gaster.

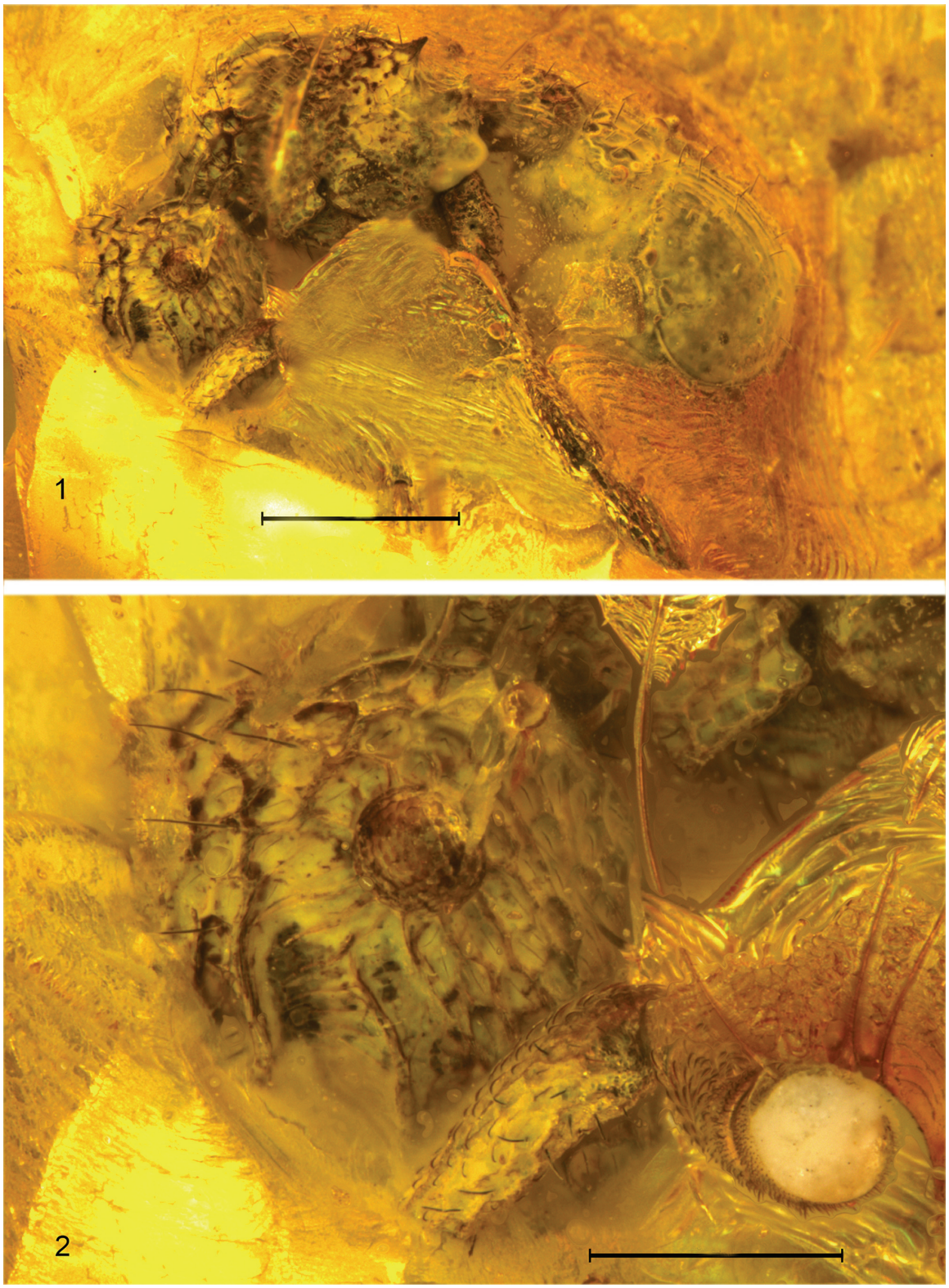
Indices include:

SI = SL/HL,
OI = OL/HL,
PI-1 = PL/PH,
PI-2 = PL/HL,
PPI = PPL/PPH,
MI = ML/MH,
ESLI = ESL/HL,
HTLI = HTL/ML.

Results

The description and drawings of *Agroecomyrmex duisburgi* by Wheeler (1915) are accurate and quite complete (see the Discussion section for some of our additions to its morphology). Workers and queens of this species clearly differ from any other ants with a two-segmented waist found in late Eocene European ambers, primarily by a downturned gaster with a sting directed at a forward angle, the presence of well-developed antennal scrobes, and by the position of the eyes at the posterior apex of the scrobes (Figs 1–2; see also Wheeler 1915, Fig. 22).

Measurements (in mm) and indices of various morphological features of the Rovno amber specimen of *A. duisburgi* (collection No. F-652) were as follows: total length ~5.5, HL 1.25, SL 1.04, OL 0.29, ML 1.82, MH 1.04, PL 0.60, PH 0.52, PPL 0.47, PPH 0.78, ESL 0.21, HTL 0.78; indices: SI 0.80, OI 0.22, PI-1 1.15, PI-2 0.46, PPI 0.60, MI 1.75, ESLI 0.16, HTLI 0.43.



Figures 1–2. *Agroecomyrmex duisburgi* Wheeler, worker: (1) body, lateral view; (2) head, lateral view. Scale bars – 1 mm.

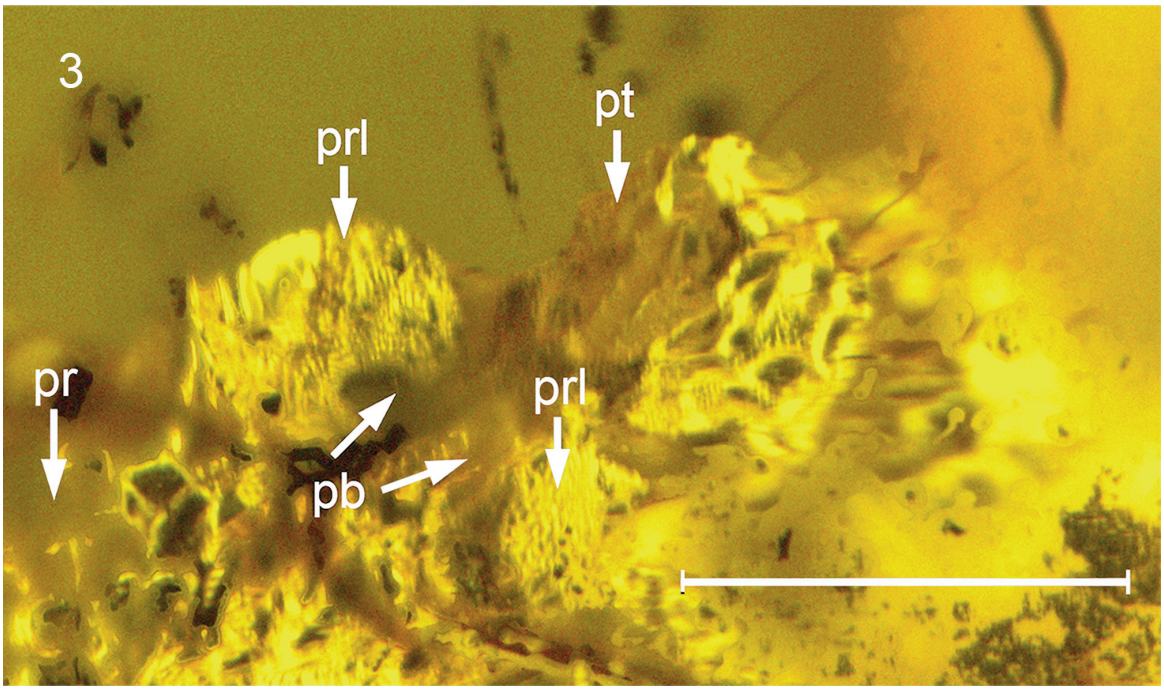


Figure 3. *Agroecomyrmex duisburgi* Wheeler, worker, propodeal lobes and petiole, dorso-lateral view; pr – propodeum, prl – propodeal lobes, pt – petiole, pb – propodeal 'bag'. Scale bar – 0.5 mm.

Discussion

To date, a combined total of 176 described species from 63 genera and 12 subfamilies have been recorded from late Eocene European ambers (i.e., Baltic, Danish, Bitterfeld, and Rovno) (Dlussky and Rasnitsyn 2009, Perkovsky 2016, Radchenko and Dlussky 2016, 2018a, 2018b, 2019, Radchenko *et al.* 2018, Radchenko and Perkovsky 2020, Radchenko and Khomych 2020, Radchenko 2020, 2021, Radchenko *et al.* 2021, Radchenko and Proshchalykin 2021). The known myremcofauna of Rovno amber is also quite diverse; including *A. duisburgi* increases the number of reported ants to 78 species in 40 genera from 10 subfamilies. Our discovery of *A. duisburgi* in Rovno amber indicates that Agroecomyrmecinae were distributed in the late Eocene on both the northern and southern coasts of the Paratethys Sea.

There have been major disagreements on the taxonomic status of Agroecomyrmecinae. All Agroecomyrmecinae species known have a two-segmented waist with well differentiated petiole and postpetiole, and based on this character Wheeler (1910, 1915) classified *Agroecomyrmex* in the subfamily Myrmicinae Lepeletier, 1835. Carpenter (1930) later established the tribe Agroecomyrmicini (*sic*) within Myrmicinae to accommodate *Agroecomyrmex* and the newly established genus *Lithomyrmex* (replacement name – *Eulithomyrmex* Carpenter, 1935), described from the Florissant shales (USA, Colorado, uppermost Eocene, ~34 Ma). Brown and Kempf (1968) described the modern genus *Tatuidris* from South America, assigned it to Agroecomyrmecini, and provided the first detailed diagnosis of this tribe based on extant and extinct genera. Agroecomyrmecini was considered a tribe of Myrmicinae until Bolton (2003) raised it to the subfamily rank, as the myrmicomorph subfamily.

Molecular phylogenetic studies, however, concluded that *Tatuidris* was not closely related to Myrmicinae, but instead related to the poneroid clade, consisting of the subfamilies Agroecomyrmecinae, Amblyoponinae, Apomyrminae, Paraponerinae, Ponerinae, and Proceratiinae (Brady *et al.* 2006, Moreau *et al.* 2006, Rabeling *et al.* 2008, Moreau and Bell 2013, Branstetter *et al.* 2017, Blanchard and Moreau 2017, Borowiec *et al.* 2019). In the first genetic analysis that included *Ankylomyrma*, Ward *et al.* (2015) concluded that it is a poneroid sister taxon to *Tatuidris*, and transferred *Ankylomyrma* to Agroecomyrmecinae.

In fact, Agroecomyrmecinae ants have a downturned gaster with a sting directed at a forward angle, traits found in some poneroids (e.g., Proceratiinae Emery, 1895 and many *Gnamptogenys* Roger, 1863), but never in Myrmicinae.

Using cladistic analysis of morphological characters, Baroni Urbani and de Andrade (2007) returned Agroecomyrmecini to Myrmicinae. Keller (2011) located *Tatuidris* in common clad with the Myrmicinae, but

considered Agroecomyrmecinae to be a separate ant subfamily. However, based on the morphological analysis of the mesosomal structure, Keller *et al*. (2014) concluded that *Tatuidris* is not related to Myrmicinae and placed it within the poneroid clade as the sister taxon of Paraponerinae, a monotypic subfamily consisting of the giant „bullet ant," *Paraponera clavata* (Fabricius, 1775) from the Neotropics. In the most recent molecular genetic analysis Borowiec *et al*. (2019) supported this view and estimated that the Agroecomyrmecinae + Paraponerinae clade separated from its sister group, the Ponerinae, ~84 Ma, Agroecomyrmecinae separated from Paraponerinae ~71 Ma, while the ancestors of *Tatuidris* and *Ankylomyrma* separated ~45 Ma, i.e., long before any known Agroecomyrmecinae fossils.

Fisher and Bolton (2016) provided additional morphological evidence for assigning *Ankylomyrma* and *Tatuidris* to Agroecomyrmecinae, and showed that these genera are poneroid. Their poneroid morphological characters include: a) the tergite and sternite of the abdominal segment IV (first gastral) are completely fused and immobile relative to each other (fused in the vast majority of poneroids and never in Myrmicinae); b) the tergite of helcium overlaps its sternite laterally (as in poneroids, in Myrmicinae the tergite and sternite are always fused into a ring); and c) the metapleural gland orifice is a simple rounded hole (usual in poneroids; a longitudinal slit or narrow crescent, opening dorsally or posterodorsally in Myrmicinae) (see also Bolton 2003). In addition, the forewing venation of *Agroecomyrmex* and *Eulithomyrmex* have four closed cells, which is a plesiomorphic state for ants in general (Dlussky 1983) and is very common in poneroids. Most modern Myrmicinae have reduced forewing venation to some extent, but many extinct and some extant genera also have a "complete" set of closed cells (Dlussky and Radchenko 2009, Dlussky *et al*. 2015).

Analyzing the morphology of extinct Agroecomyrmecinae offers a variety of clues regarding the ecology of these ants. Dlussky and Fedoseeva (1988) emphasized that the evolution of organs or structures in living organisms cannot be considered in isolation from the functional system (i.e., the system of organs and structures connected by dynamic coordination and performing one complex function) in which they are included. Below we consider the main structural peculiarities of the extinct Agroecomyrmecinae, especially of the head, mesosoma and metasoma.

First, both *Agroecomyrmex* and *Eulithomyrmex* were already fairly specialized morphologically. The initial for ants can be considered a suboval head without distinct occipital corners and a widely rounded posterior margin, without antennal scrobes, with eyes of moderate size, located approximately at the midlength of the sides of the head, and antennal sockets are open (Dlussky and Fedoseeva 1988). However, both genera have well-developed antennal scrobes, and their eyes are located at the posterior apex of the scrobes. Antennal scrobes are developed in many Myrmicinae and in some Ectatomminae Emery, 1895 and Dorylinae Leach, 1815 genera, but a somewhat similar combination of deep scrobes with posterior position of eyes is found only in *Cephalotes* Latreille, 1802 (Myrmicinae) and ectatommine genus *Aulacopone* Arnoldi, 1930. Interestingly, by some other features, *Aulacopone* somewhat resembles *Agroecomyrmex*, in particular, by a wide petiole with a large ventral lobe, and especially by the tip of the gaster directed downward and somewhat forward, but distinctly distinguishes from the latter genus by the absence of an isolated postpetiole. However, this similarity is almost certainly due to convergence.

Nevertheless, the general head shape of *Agroecomyrmex* and *Eulithomyrmex* is quite common in many modern ants. It is subrectangular, with very slightly convex or almost straight sides, narrowly rounded occipital corners and an almost straight posterior margin, and antennal sockets are partly concealed by the frontal lobes. The mandibles are also unmodified, subtraingular, stout, with a well-developed masticatory margin, possessing several subequal teeth.

On the whole, the mesosoma of *Agroecomyrmex* workers is also not very strongly modified, although with the completely fused and inconspicuous promesonotal suture and with the shallow but distinct metanotal groove. Complete fusion of the promesonotal suture is characteristic for all Myrmicinae; even if in some species it is visible on the mesosomal dorsum, the pronotum and mesonotum are unable to move relative to each other. However, this suture is also fused in most dorylomorphs and in the poneroids subfamilies Ectatomminae, Paraponerinae Emery, 1901 and Proceratiinae (Bolton 2003), which may indicate the independent development of this trait in different evolutionary groups of ants.

On the other hand, the posterior (declivous) surface of the propodeum together with the propodeal lobes forms a quite peculiar structure in *Agroecomyrmex*, which most likely has a biomechanical significance (see below). The declivous surface is concave, but this concavity is not like that in some other ant genera (e.g., *Dolichoderus* Lund, 1831 or *Lepisiota* Santschi, 1926). This surface is slightly concave not only anteriorly, but also to the sides, and forms a kind of wide tubular groove open from above. At the same time, the propodeal lobes are very strongly developed, large, high, and flat, projecting posteriorly beyond the declivous surface of the propodeum, so that they even slightly cover the petiolar node laterally. Ventrally, they are separated from each other by an elongated groove reaching the lower posterior edge of the propodeal declivity. The petiolar peduncle is relatively short, but very thin compared to the size of the node, and when the petiole is raised up, its peduncle can

enter this groove, and its node turns into a kind of „bag" formed by the propodeal declivity and the propodeal lobes. In this case, the node is fixed in a certain way by the propodeal lobes, which should prevent its displacement to the sides (Fig. 3; see also Wheeler 1915, Fig. 22 a).

Apart from the head and mesosoma, *Agroecomyrmex* and *Eulithomyrmex* (as well as modern Agroecomyrmecinae) have a modified metasoma compared to poneroids. First, they have a distinct two-segmented waist with a postpetiole distinctly isolated from the gaster, as in Myrmicinae and some other ant subfamilies, which clearly distinguishes them from poneroids (which is why they were previously assigned to Myrmicinae). The vast majority of poneroids have a girdling constriction between the first and second gastral (III and IV abdominal) segments, with developed pretergite and presclerite on segment IV. The first gastral segment in poneroids may be the same size as the second, or larger, or somewhat smaller than the latter. However, in *Paraponera clavata* (Fabricius, 1775) and some *Proceratium* Roger, 1863 species the first gastral segment is definitely smaller than the second and looks intermediate between the "typical postpetiole" and the "proper" first gastral segment. A similar size of the first gastral segment is found in some Dorylinae genera or in the fossil Myrmeciinae genus *Prionomyrmex* Mayr, 1868. Interestingly, *Tatuidris* has been considered as a sister group to *Paraponera clavata* in many molecular genetic studies (Brady *et al.* 2006, Moreau *et al.* 2006, Ward *et al.* 2015). Perhaps this is not accidental?

In principle, the question of whether to call the III abdominal segment "the postpetiole" or "the first gastral segment" is rather terminological, since the character of the articulations of this segment both with the previous one and with the subsequent one, does not fundamentally differ.

Bolton (1990a,b,c, Baroni Urbani *et al.* 1992) studied in detail the abdominal structure of ants and discussed their phylogetic significance, and Dlussky and Fedoseeva (1998) and Fedoseeva (2008) considered the importance of modifications of the external structure and anatomy of the abdominal segments from an evolutionary-morphological point of view.

The transformation of the abdominal segment III into a genuine postpetiole in Agroecomyrmecinae does not conflict with the general structural plan of poneroids, which already have pretergite and presternite on abdominal segment III. This required only the miniaturization of this segment simultaneously with a gradual decrease in the size of its pretergite and presternite and their transformation into a true helcium, and does not require complex coordinated morphofunctional rearrangements of organ systems. Moreover, in the fossil and extant Agroecomyrmecinae genera the postpetiole is widely attached to the first gastral segment and the helcium should have a rather large diameter (e.g., see *T. tatusia* photomicrographs: antweb.org/specimenImages.do?name=antweb1008593).

Little can be added to the morphological characteristics of *Eulithomyrmex*. Like other agroecomyrmecines, its representatives have a two-segmented waist, widely attached to the gaster, and a modified, curved down gaster with a tip directed downward and forward. However, their antennae have a two-segmented club, which is an indisputable apomorphy compared to the three-segmented one of *Agroecomyrmex*. Finally, both *Eulithomyrmex* species are noticeably larger than all other known species of this subfamily: the body length of gynes is 8 mm, of males 7 mm, of worker 6 mm (Carpenter 1935).

Compared to the fossil Agroecomyrmecinae, modern *Tatuidris* and *Ankylomyrma* appear to be much more specialized. Workers and gynes of *Tatuidris tatusia* have seven-segmented antennae with a well developed two-segmented club (in males, the antennae are 12-segmented with a filiform funiculus without a club); their head dorsum is a shield-shaped with eyes and antennae located below this shield, as in some Myrmicinae genera, e.g. *Phalacromyrmex* Kempf, 1960 and some Attini F. Smith, 1858 (sensu Ward *et al.* 2015), but such a structure has never been observed in poneroids. The forewing venation of gynes and males is also more derived compared to fossil genera, in particular, the cross-vein rs-m is completely reduced and the cell rm is open (Donoso 2012).

Ankylomyrma coronacanta Bolton, 1973 seems to be even more specialized. The occipital margin of its head is bordered by a vertical lamella, equipped with numerous dentiform processes, similar to a kind of crown (hence the name of this species); the mesosoma and petiole also have spines and dents of various length. In addition, its gaster is extremely peculiar and has no analogues among other ants: it consists almost entirely of an enormously enlarged and strongly vaulted first tergite. The first gastral sternite is reduced to a narrow rim, and the remaining gastral segments are telescopically inserted inside, so the well-developed sting is directed forward below the waist (Bolton 1973).

Tatuidris tatusia is a typical cryptic dweller of leaf litter in tropical forests from Mexico to Brazil and Peru. Based on the peculiarities of its morphology, this species should have quite special diet, but its food preferences remain unknown: in artificial nests in the laboratory, the workers refused any food offered to them, including a wide variety of arthropods collected in the species' nesting sites, as well as sugar syrup and protein food (Donoso 2012).

Even less known is the lifestyle of the Afrotropical *A. coronacanta*. Bolton (1973), based on its morphology and collecting sites, suggested that it might be an arboreal dweller. In any case, it is definitely not inhabitant of a leaf litter.

The possible lifestyle of the fossil *Agroecomyrmex duisburgi* or *Eulithomyrmex* species can only be

guessed from their morphological features. The general plan of the head structure in *A. duisburgi*, *Eulithomyrmex* and *Ankylomyrma* is similar: it is subrectangular, with well developed and non-specialized mandibles, with deep antennal scrobes, a short and thick antennal scape and not long funiculus, and an extremely posterior position of the well-developed, subcircular and protruding eyes. Most likely, when the workers moved, the head was carried at a right or slightly obtuse angle to the long axis of the body. If so, then the field of view could be quite wide, the ants could look forward, sideways, up and down, and probably even a little backwards, which can give it advantages both in searching for prey and defending against predators. The mesosoma in *Agroecomyrmex* is short and compact, and the legs are also relatively short. The most conspicuous is the structure of the metasoma with the tip of the gaster directed downward and somewhat forward.

All of the above features may indicate that the workers of *Agroecomyrmex* were most likely not dwellers of leaf litter: when moving in the litter, the head should be directed forward rather than down, but in this case, the location of the eyes seems useless, since with such a position of the head the ant most likely will not be able to see what is in front and below it. In contrast, the leaf litter dweller *Tatuidris tatusia* has much smaller eyes located below the dorsal shield of the head, and the ant would not be able to look forward when its head was pointing down. *Agroecomyrmex duisburgi* may have had been able to curl up into a ball when threatened, like *Ankylomyrma* or many other modern ants (e.g., *Myrmecina* Curtis, 1829).

Based on its rarity in the representative collection and on overall morphology, we suggest that *A. duisburgi* was not arboreal but rather epigean, building nests in soil or woody debris, and foraging on the soil surface or on fallen leaves or needles. When hunting, the workers could keep the waist slightly raised up, fixed in the propodeal "bag" (see above), the gaster was somewhat elevated above the surface, which did not interfere with movement, and its tip was directed rather downward. They could grab prey with their mandibles, and then bend the gaster down and even twist it around the long axis of the body due to the presence of tubular connections both between the petiole and the postpetiole and the postpetiole and the first gastral segment, and stung the victim.

Many interesting questions remain concerning Agroecomyrmecinae, and much work remains. For example, where did they originate and how did they spread to have representatives in South America, North America, Europe, and Africa? What were paths of morphological evolution of Agroecomyrmecinae? Agroecomyrmecinae can be considered an important link in the evolution of both Myrmicinae and poneroids, and a detailed study of the morphology, anatomy, behaviour and lifestyle of modern species of this subfamily is important for understanding the paths and directions of ants' evolution in general.

Acknowledgements

We are sincerely grateful to Jonas Damzen (Lithuania) and Eugeny Perkovsky (Ukraine) for providing the specimen (JDK 4522) for the investigation, and to James K. Wetterer (USA) for valuable comments to the manuscript and correction English. This work was supported by the grant NRFU (Ukraine) No. 2020/02/0369 (to A. Radchenko).

References

Baroni Urbani, C., Bolton, B. and P. S. Ward. 1992. The internal phylogeny of ants. Systematic Entomology, 17: 301–329.

Baroni Urbani, C. and M. L. de Andrade. 2007. The ant tribe Dacetini: limits and constituent genera, with descriptions of new species. Annali del Museo Civico di Storia Naturale "G. Doria", 99: 1–191.

Blanchard, B. D. and C. S. Moreau. 2017. Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. Evolution, 71: 315–328. doi:10.1111/evo.13117.

Bolton, B. 1973. A remarkable new arboreal ant genus from West Africa. Entomologist's Monthly Magazine, 108: 234–237.

Bolton, B. 1990a. Abdominal characters and status of the cerapachyine ants. Journal of Natural History, 24: 53–68.

Bolton, B. 1990b. The higher classification of the ant subfamily Leptanillinae. Systematic Entomology, 15: 267–282.

Bolton, B. 1990c. Army ants reassessed: the phylogeny and classification of the doryline section. Journal of Natural History, 24: 1339–1364.

Bolton, B. 2003. Synopsis and classification of Formicidae. Memoirs of the American entomological Institute, 71: 1–370.

Borowiec, M. L., Rabeling, C., Brady, S. G., Fisher, B. L. and P. S. Ward. 2019. Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. Molecular Phylogenetics and Evolution, 134: 111–121. https://doi.org/10.1016/j.ympev.2019.01.024.

Brady, S. G., Schultz, T. R., Fisher, B. L. and P. S. Ward. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. Proceedings of the National Academy of Sciences U.S.A, 103: 18172–18177. doi: 10.1073/pnas.0605858103.

Branstetter, M. G., Longino, J. T., Ward, P. S. and B. C. Faircloth. 2017. Enriching the ant tree of life: enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. Methods in Ecology and Evolution, 8: 768–776. doi: 10.1111/2041-210X.12742.

Brown, W. L. and W. W. Kempf. 1968. *Tatuidris*, a remarkable new genus of Formicidae. Psyche, 74: 183–190.

Carpenter, F. M. 1930. The fossil ants of North America. Bulletin of the Museum of Comparative Zoology, 70: 1–66.

Carpenter, F. M. 1935. A new name for *Lithomyrmex* Carp. (Hymenoptera). Psyche, 42: 91.

Dlussky, G. M. 1983. [A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and the scolioids]. Paleontologicheskii Zhurnal, 17: 65–78. (In Russian).

Dlussky, G. M. and E. B. Fedoseeva. 1988. [Origin and early stages of the ant evolution (Hymenoptera: Formicidae)]. Melovoj biocenoticheskij krizis i evolucija nasekomych. Moskva: Nauka Publ: 70–144. (In Russian).

Dlussky, G. M. and A. Radchenko. 2009. Two new primitive ant genera from the European amber (late Eocene). Acta Palaeontologica Polonica, 54: 435–441. doi: 10.4202/app.2008.0092.

Dlussky, G. M. and A. P. Rasnitsyn. 2009. Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. Paleontological Journal, 43: 1024–1042. https://doi.org/10.1134/S0031030109090056.

Dlussky, G. M., Rasnitsyn, A. P. and K. S. Perfilieva. 2015. The Ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (Late Eocene of Sikhote-Alin, Russian Far East). Caucasian entomological bulletin, 11: 131–152. https://doi.org/10.23885/1814-3326-2015-11-1-131-152.

Donoso, D. A. 2012. Additions to the taxonomy of the armadillo ants (*Tatuidris*). Zootaxa, 3505: 61–81.

Fedosseva, E. B. 2008. [Technological approach to insect anatomy and evolution]. Zhurnal obshchej biologii, 69: 264–283. (In Russian).

Fisher, B. L. and B. Bolton. 2016. Ants of the world. Ants of Africa and Madagascar. A guide to the genera. University of California Press, 503 pp.

Keller, R. A. 2011. A phylogenetic analysis of ant morphology with special reference to the poneromorph subfamilies. Bulletin of the American Museum of Natural History, 355: 1–90. doi: 10.1206/355.1.

Keller, R. A., Peeters, Ch. and P. Beldade. 2014. Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. eLIFE, 3: 1–19. doi: 10.7554/eLife.01539.

Moreau, C. S. and C. D. Bell. 2013. Testing the museum versus cradle tropical biological diversity hypotheses: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution, 67: 2240–2257. doi:10.1111/evo.12105.

Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B. and N. E. Pierce. 2006. Phylogeny of the ants: diversification in the age of angiosperms. Science, 312: 101–104.

Perkovsky, E. E. 2016. Tropical and Holarctic ants in Late Eocene ambers. Vestnik zoologii, 50: 111–122. https://doi.org/10.1515/vzoo-2016-0014.

Rabeling, C., Brown, J. M. and M. Verhaagh. 2008. Newly discovered sister lineage sheds light on early ant evolution. Proceedings of the National Academy of Sciences U.S.A, 105(30): 14913–14917. doi: 10.1073/pnas.0806187105.

Radchenko, A. 2020. New species of extinct ant genus *Eocenomyrma* Dlussky et Radchenko (Hymenoptera: Formicidae: Myrmicinae) from the Baltic amber. Annales Zoologici, 70: 109–111. https://doi.org/10.3161/00034541ANZ2020.70.1.005.

Radchenko, A. G. 2021. New species of the fossil ant genus *Drymomyrmex* (Hymenoptera, Formicidae, Formicinae) form the late Eocene Rovno amber (Ukraine). Palaeoentomology, 4: 544–549. https://doi.org/10.11646/palaeoentomology.4.6.4.

Radchenko, A. G. and G. M. Dlussky. 2016. Further data on the extinct ant genus *Eocenomyrma* (Hymenoptera, Formicidae). Vestnik zoologii, 50: 395–406. https://doi.org/10.1515/vzoo-2016-0046.

Radchenko, A. G. and G. M. Dlussky. 2018a. Ants of the genus *Fallomyrma* Dlussky et Radchenko (Hymenoptera, Formicidae, Myrmicinae) from Late Eocene European Ambers. Paleontological Journal, 52: 155–163. https://doi.org/10.1134/S0031030118020107.

Radchenko, A. and G. M. Dlussky. 2018b. Two new fossil species of the ant genus *Pristomyrmex* Mayr (Hymenoptera, Formicidae) from the Rovno and Bitterfeld ambers. Annales Zoologici, 68: 251–258. https://doi.org/10.3161/00034541ANZ2018.68.2.004.

Radchenko, A. and G. M. Dlussky. 2019. The first record of the ant genus *Crematogaster* (Hymenoptera, Formicidae) from the late Eocene European amber. Annales Zoologici, 69: 417–421. https://doi.org/10.3161/00034541ANZ2019.69.2.008.

Radchenko, A, Dlussky, G. M. and K. S. Perfilieva. 2018. A new extinct ant genus (Hymenoptera, Formicidae, Myrmicinae) from the Late Eocene Rovno amber – a putative ancestor of the *Leptothorax* genus group. Myrmecological News, 27: 111–117. https://doi.org/10.25849/myrmecol.news_027:111.

Radchenko, A. G, and M. R. Khomych. 2020. Ants of the extinct genus *Cataglyphoides* Dlussky (Hymenoptera: Formicidae: Formicinae) from the late Eocene European ambers. Invertebrate Zoology, 17: 154–161. https://doi.org/10.15298/invertzool.17.2.05.

Radchenko, A. G, and M. R. Khomych. In press. First records of aneuretine ants (Hymenoptera: Formicidae: Aneuretinae) in late Eocene Rovno amber (Ukraine).

Radchenko, A. G. and E. E. Perkovsky. 2020. New finds of the fossil ant genus *Prionoyrmex* Mayr (Hymenoptera, Formicidae, Myrmeciinae) in Late Eocene European Ambers. Paleontological Journal, 54: 617–626. https://doi.org/10.1134/S0031030120060088.

Radchenko, A. G., Perkovsky, E. E. and D. V. Vasilenko. 2021. *Formica* species (Hymenoptera, Formicidae, Formicinae) in late Eocene Rovno amber. Journal of Hymenoptera Research, 82: 237–251. https://doi.org/10.3897/jhr.82.64599.

Radchenko, A. G. and M. Yu. Proshchalykin. 2021. New extinct ant genus (Hymenoptera, Formicidae, Myrmicinae) from late Eocene Rovno amber. *In*: Proshchalykin, M, and V. Gokhman (Eds). Hymenoptera studies through space and time: A collection of papers dedicated to the 75th anniversary of Arkady S. Lelej. Journal of Hymenoptera Research, 84: 271–282. https://doi.org/10.3897/jhr.84.65238.

Ward, P. S., Brady, S. G., Fisher, B. L. and T. R. Schultz. 2015. The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade. Systematic Entomology, 40: 61–81.

Wheeler, W. M. 1910. Three new genera of myrmicine ants from tropical America. Bulletin of the American Museum of Natural History, 28: 259–265.

Wheeler, W. M. 1915. The ants of the Baltic Amber. Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg in Preußen, 55: 1–142. https://www.antwiki.org/wiki/images/e/ec/Wheeler_1915i.pdf.